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Ray W. Drenner, John R. Mummert, Frank deNoyelles, Dean Kettle

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Selective Particle Ingestion by a Filter-Feeding Fish and Its Impact on Phytoplankton Community Structure

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Selective particle ingestion by a filter-feeding fish and its impact on phytoplankton community structure[1]

Ray W. Drenner and John R. Mummert
Biology Department, Texas Christian University, Fort Worth 76129

Frank deNoyelles, Jr., and Dean Kettle
Department of Systematics and Ecology, University of Kansas, Lawrence 66045

Abstract

The ingestion rates of filter-feeding gizzard shad for different sizes of suspended particles were measured using mixtures of microspheres and zooplankton. Ingestion rate increases as a function of particle size, leveling off at 60 μm. The particle-size-dependent ingestion rates were consistent with a model of filtering efficiency based on the cumulative frequency of interraker distances of gizzard shad gill rakers.

Comparison of ponds containing gizzard shad with control ponds without fish showed that gizzard shad suppressed Ceratium, the only phytoplankton species large enough to be ingested at a maximum rate. Gizzard shad did not have a significant effect on populations of Synedra, Peridinium, Navicula, Kirchneriella, Cyclotella, and Chlamydomonas. Populations of Ankistrodesmus, Cryptomonas, Cosmarium, Rhodomonas, and algae and bacteria from 2–4 μm were enhanced by gizzard shad.

Most studies of grazer impact on freshwater phytoplankton communities have focused on zooplankton. Herbivorous zooplankton usually feed on nannoplankton <50 μm in diameter (Porter 1977; Briand and McCauley 1978; Geller and Müller 1981). Because of their unavailability to zooplankton, some limnologists have assumed that net phytoplankton are dead ends in the planktonic food webs of temperate zone lakes (Porter 1977). This food web concept ignores field studies showing that several species of North American fish consume filamentous and colonial algae (Murphy 1950; Kutkuhn 1957; Starostka and Applegate 1970; Baker and Schmitz 1971; Gunn et al. 1977). We present evidence here of selective ingestion of net phytoplankton by a freshwater fish, the gizzard shad (Dorosoma cepedianum). The gizzard shad and threadfin shad (D. petenense) often dominate the standing crops of fish in central U.S. reservoirs (Jenkins 1967). Gizzard shad >2.5 cm standard length (SL) feed on detritus, phytoplankton, and zooplankton (Drenner et al. 1982a). These omnivorous fish are pump filter feeders, capturing food with a series of suctions not visually directed at individual particles (Drenner et al. 1982b).

We hypothesized that the gizzard shad's selective grazing on phytoplankton is determined by the filtering efficiency of its gill rakers, simple comblike structures (Fig. 1) free of the large accessory teeth found between the rakers in some fishes (Fryer and Iles 1972; Iwata 1976; Starostka and Applegate 1970; Blaber 1979). Fish gill rakers are thought to function as mechanical filters (Durbin and Durbin 1975; Rosen and Hales 1981). We developed a model of filtering efficiency as a cumulative frequency of interraker distances (Boyd 1976; Nival and Nival 1976) and used the model to predict gizzard shad feeding rates on different sizes of microspheres and zooplankton. We determined the impact of gizzard shad grazing on phytoplankton community structure from changes in the plankton of experimental ponds after introduction of the fish.
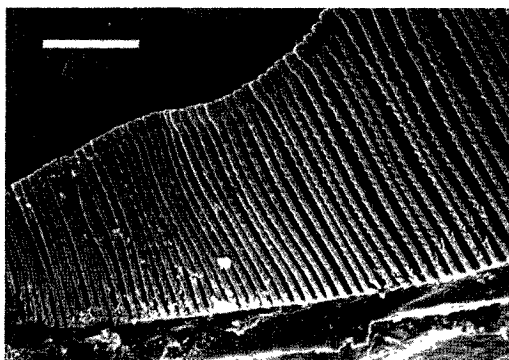
Fig. 1. Scanning electron photomicrograph of the anterior surfaces of the gill rakers on the first gill arch of a 15.2-cm-SL gizzard shad. Bar—1 mm.

the University of Oklahoma Biological Station use of laboratory facilities, and the University of Kansas Nelson Environmental Study Area use of the experimental pond.

Methods

We determined the cumulative frequencies of interraker distances of five Formalin-preserved gizzard shad ranging from 13.6- to 16.3-cm SL. After dissecting all the gill arches from one of the opercular cavities of a fish, the rows of rakers were stripped from the gill arches, placed in water droplets on microscope slides, and interraker distances measured with a Wild inverted microscope.

We assumed that the relative contribution of an interraker space to the filtering efficiency of an individual shad is proportional to the length of the gill rakers bordering the space. Long gill rakers and the spaces between them present a larger filtering surface area than shorter gill rakers. To weight the interraker spaces for gill raker length, the gill raker surfaces were treated as a series of trapezoidal areas with bases of 1,490 μm and sides equal to the lengths of the bordering gill rakers. We determined a representative interraker distance for each trapezoidal area as the mean of three interraker spaces in the center of the trapezoid and computed the cumulative frequency distribution of interraker distances, weighting each distance by its trapezoid area relative to the total filtering surface area.

We tested our model by predicting the

feeding rates of gizzard shad feeding in an 80-liter pool. Two gizzard shad, 13.6- and 16.3-cm SL, were used in each of four feeding trials. They were fed a mixture of microspheres (Ionics, Inc., Watertown, Mass.), copepod nauplii, and the rotifer *Keratella* sp. which gizzard shad can capture with an efficiency approaching 100% (Drenner et al. 1982*a*). Microsphere diameters ranged from 10 to 80 μm. Mean copepod nauplius body length was 185.5 μm (SD = 38.0) and width was 95.4 μm (SD = 25.5). Mean *Keratella* body length (including spines) and width were 118.0 μm (SD = 29.0) and 78 μm (SD = 23.5). An equal weight of 0.0025 g of each of six microsphere size classes was used in an experiment. Initial numbers per liter were: 10–20-μm spheres (27,645), 20–30-μm (16,050), 30–40-μm (2,330), 40–50-μm (708), 50–60-μm (637), 70–80-μm (210), nauplii (504), and *Keratella* (725). We assumed that three airstones, stirring every 10 min, and the swimming movements of the fish kept the particles in the pool well mixed. Fishless control pools with zooplankton and microspheres allowed us to account for microsphere loss due to zooplankton grazing.

To test our model, we compared declines in microsphere and zooplankton densities predicted by the model with observed changes. We measured the decrease in density with two replicate samples taken at 0 and 1.0 h. A rubber stopper was randomly placed on the pool floor and a tube of 6.9-cm i.d. quickly lowered onto the stopper. The plugged tube was removed, the volume of water measured, and the contents preserved in Formalin. Microspheres and zooplankton were counted and measured with a Wild inverted compound and Nikon stereomicroscope.

To compute the predicted changes in particle densities we used the equation:

$$N_t = N_0 \exp(-Kt)$$

where N_t is the number of particles at a time t, N_0 is the number of particles at time 0, t is the duration of the experiments (hours), and K is the coefficient of grazing. N_t was corrected for the slight loss of microspheres in the controls. K is computed as

$$K = V_f F V_p^{-1}$$

where V_f is the total volume inhaled by the two fish during time t, F is the filtering efficiency, and V_p is the pool volume (80 liters). The total volume inhaled by each fish was computed with the equation

$$FR = 0.00324SL^{2.08}$$

where FR is filtering rate (liters·min^{-1}) (Drenner et al. 1982b). Because the cumulative frequency distribution of interraker distances acts as a probability function for retention efficiency, we computed the filtering efficiency, F, for various particle sizes as the mean cumulative frequency of interraker distance of the five gizzard shad examined.

We studied the impact of the selective grazing of gizzard shad on a natural phytoplankton community in a field experiment using a pond divided by concrete partitions into four 0.006-ha, 61-m³ mud-bottomed quadrants. Gizzard shad from 8- to 20-cm SL were electrofished from Lone Star Lake, Douglas County, Kansas, and stocked into two of the quadrants at densities of 233 and 257 kg·ha^{-1} on 25 June 1978 (*see* Drenner et al. 1982a). Phytoplankton samples were collected with a column sampler (deNoyelles and O'Brien 1978). On each sampling date, two column samples were taken in each quadrant, mixed together, and a 125-ml subsample was preserved with Lugol's iodine. Phytoplankton samples were concentrated for 4 days in settling chambers 12.5 mm in diameter and counted with a Wild inverted microscope with detection limits of 2–10 organisms·ml^{-1}. Organisms <2 μm were not counted. Treatment effects from 29 June to the end of the experiment were analyzed with a split-plot analysis of variance (ANOVA for repeated measures) (Winer 1971; Gill 1978). Because the original analysis of shad effects on zooplankton (Drenner et al. 1982a) was statistically invalid, we also reanalyzed the zooplankton data with a split-plot ANOVA.

Results

Interraker spaces ranged from 1 to 85 μm. The frequencies of interraker distances for the five fish examined were not significantly different according to pairwise compari-
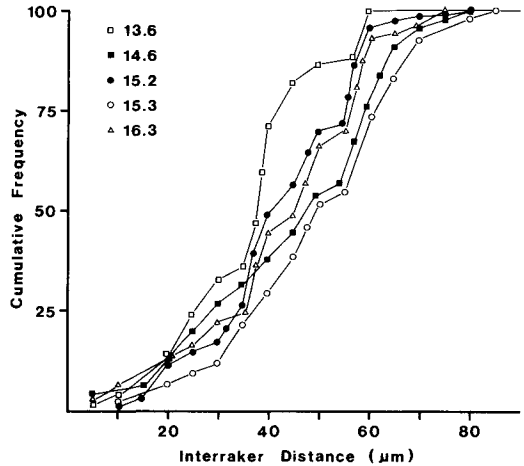

Fig. 2. Cumulative size-frequency distributions of interraker distances of gizzard shad. Numbers are fish standard lengths (cm).

sions for all possible pairs of distributions (Mann-Whitney U-test, $P < 0.05$; Sokal and Rohlf 1969). Filtering probabilities were computed as a mean of the cumulative frequencies of the interraker distances (Fig. 2).

The proportion of particles removed by fish increased as a function of particle size, leveling off at about 60 μm (Fig. 3). The predicted and observed changes in particle densities were closely correlated (Pearson product-moment correlation; $N = 15$, $r = 0.96$, $P < 0.01$; Sokal and Rohlf 1969).

The temperatures, turbidities (Fig. 4A), algal biomass (Fig. 4B), and phytoplankton densities (Fig. 5) of the fish and control ponds were similar at the beginning of the experiment. Temperature did not differ between the four ponds and ranged from 24° to 32°C. The fish ponds were more turbid than the controls from 29 June through 28 September ($P = 0.06$, df = 1,2). Fish may have increased turbidity by suspending sediments or by changing the algal community. We estimated algal biomass by computing cell volumes for each genus using mean cell dimensions given in Fig. 5. Although algal biomass was not significantly different in the fish and control ponds ($P = 0.13$, df = 1,2) (Fig. 4B), it did tend to be lower in the fish ponds, suggesting that fish suspension of sediments may have caused the turbidity increase.
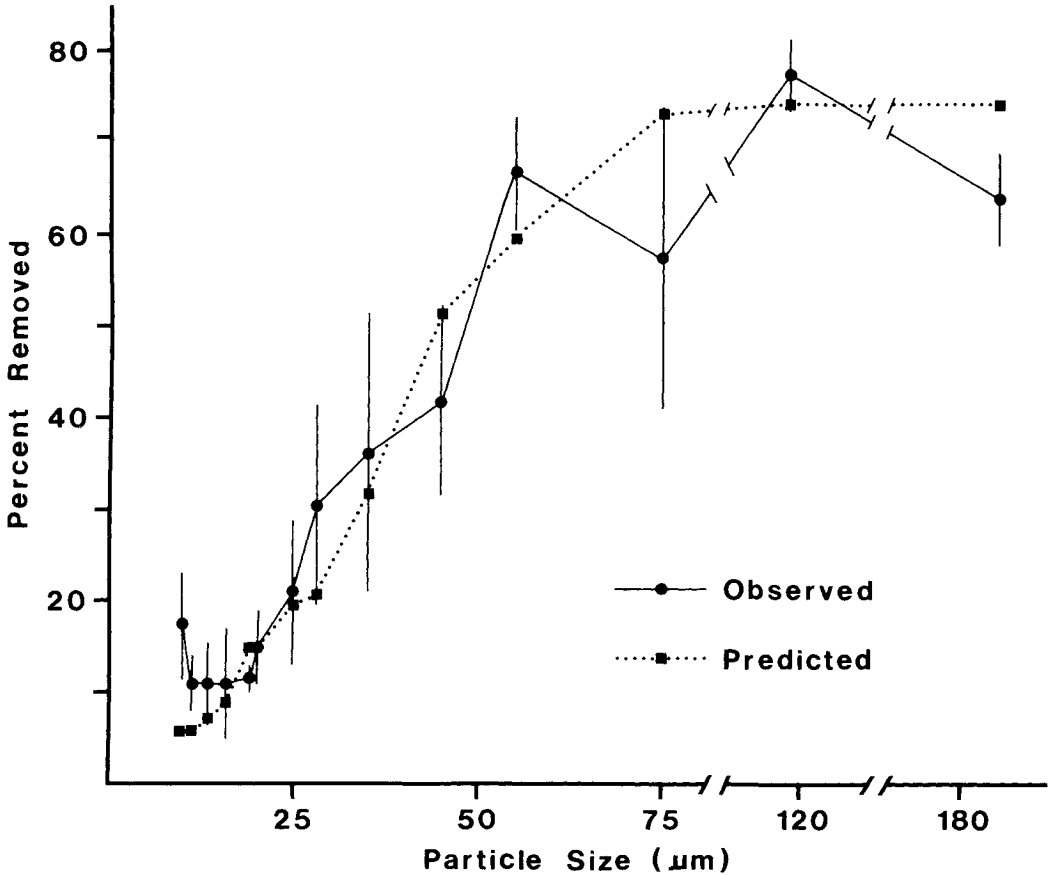
Fig. 3.   Observed removal rates of microspheres and zooplankton by filter-feeding gizzard shad compared with removal rates predicted by filtering-rate and filtering-efficiency functions. Bars—standard errors of observed removal rates ($n = 4$).

Feeding by gizzard shad significantly reduced the population of *Ceratium* but had no consistent effect on populations of *Synedra, Peridinium, Navicula, Kirchneriella, Cyclotella,* and *Chlamydomonas* (Fig. 5). Results of the ANOVA suggest that populations of *Ankistrodesmus, Cryptomonas, Cosmarium, Rhodomonas,* and 2–4-μm algae and bacteria were enhanced by the presence of fish.

Discussion

Evidence that fish can influence phytoplankton communities has come primarily from studies of visual-feeding zooplanktivorous fish and their indirect effect on phytoplankton communities. Visual-feeding fish are size-selective predators, selectively feeding on large zooplankton (Durbin 1979; O'Brien 1979). The addition of size-selective fish predators to fishless communities not only suppresses the larger zooplankton, but alters nutrient levels and increases phytoplankton standing crops (Hurlbert et al. 1972; Shapiro et al. 1975; Andersson et al. 1978; Hurlbert and Mulla 1981; Lynch and Shapiro 1981). While visual-feeding fish such as the bluegill (*Lepomis macrochirus*) may ingest filamentous algae, the algae function only as a supplemental food source during periods of low invertebrate prey abundance (Kitchell and Windell 1970).

Filter-feeding fish have a different influence on plankton community structure than visual feeders. Filter-feeding fish consume both zooplankton and phytoplankton. Fil-
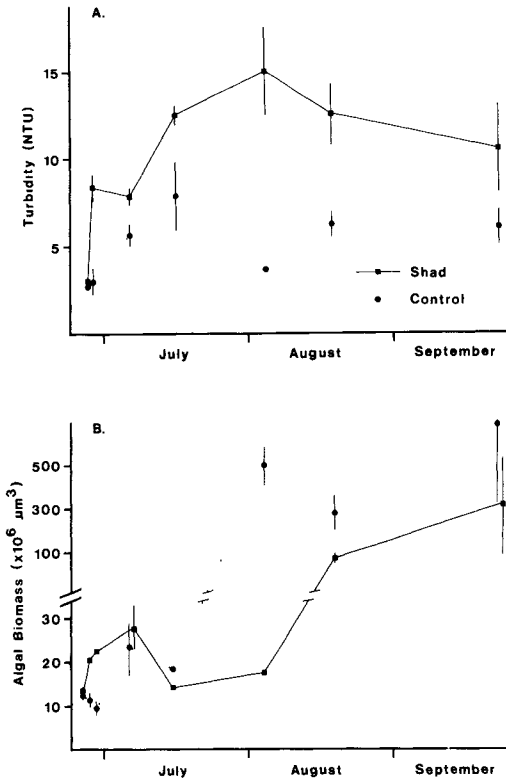
Fig. 4. Changes in turbidity and algal biomass of ponds containing gizzard shad and control ponds without fish. Points—means of replicates ponds; bars—range of observed turbidity or algal biomass.

ter feeders have highest feeding rates on or passive-feeding selectivity for the most easily captured zooplankton prey (Drenner et al. 1978, 1982a). According to our reanalysis of the zooplankton data from the same pond experiment presented here, filter-feeding gizzard shad suppressed populations of cyclopoid copepodids ($P = 0.05$), copepod nauplii ($P = 0.03$), and *Keratella* ($P = 0.04$), did not affect *Chaoborus* ($P = 0.28$) and *Diaphanosoma* ($P = 0.32$), and enhanced *Diaptomus* ($P = 0.04$) (df = 1,2).

Drenner et al. (1982a) hypothesized that filter-feeding gizzard shad would not enhance nannoplankton as did visual-feeding fish because the increase in *Diaptomus* might offset the suppression of other herbivorous zooplankton, such as *Keratella*, resulting in less change in zooplankton grazing pressure.

Contrary to that hypothesis, the nannoplankton enhancement by shad approximates that observed for visual-feeding fish (Hurlbert et al. 1972; Andersson et al. 1978; Hurlbert and Mulla 1981; Lynch and Shapiro 1981). Factors which were not monitored, such as pond nutrient levels, and shad nutrient regeneration and digestive tract enhancement may have contributed to the nannoplankton increase. Nutrient excretion by fish may increase nutrient levels (e.g. Hall et al. 1970; Lamarra 1975; *but see* Nakashima and Leggett 1980). Studies by Velasquez (1939) and Smith (1963) showed that 46 genera of algae survived passage through the digestive tract of gizzard shad, including *Ankistrodesmus, Chlamydomonas, Cosmarium, Kirchneriella,* and *Navicula.*

There has been little experimental study of the mechanisms controlling selective grazing by filter-feeding fish. Durbin and Durbin (1975) found that the feeding rate of the marine planktivore, *Brevoortia tyrannus,* was a log function of plankton size. They attributed the fish's differential feeding rates to the gill raker spacing but did not test the hypothesis. Although our study supports the Durbin hypothesis that the filtering process is mechanical, experiments in which particle biomass and quality are varied within particle size categories would be necessary to test for behavioral modification of filtering efficiency. Rosen and Hales (1981) suggested that filter-feeding paddlefish (*Polyodon spathula*) can behaviorally alter filtering efficiency.

The direct impact of gizzard shad grazing on phytoplankton is determined by fish feeding rates relative to algal growth rates. Algal growth rates generally decrease with increasing size (Banse 1976; Schlesinger et al. 1981; Smith and Kalff 1982). Because gizzard shad feeding rates are greatest for the more slowly growing large algae, gizzard shad would be most likely to directly suppress the larger algae. In our pond experiment, gizzard shad suppressed only *Ceratium,* a large dinoflagellate with a relatively slow growth rate (Sommer 1981). *Ceratium* may also be vulnerable to gizzard shad grazing pressure because it does not survive passage through shad digestive tracts (Smith 1963).
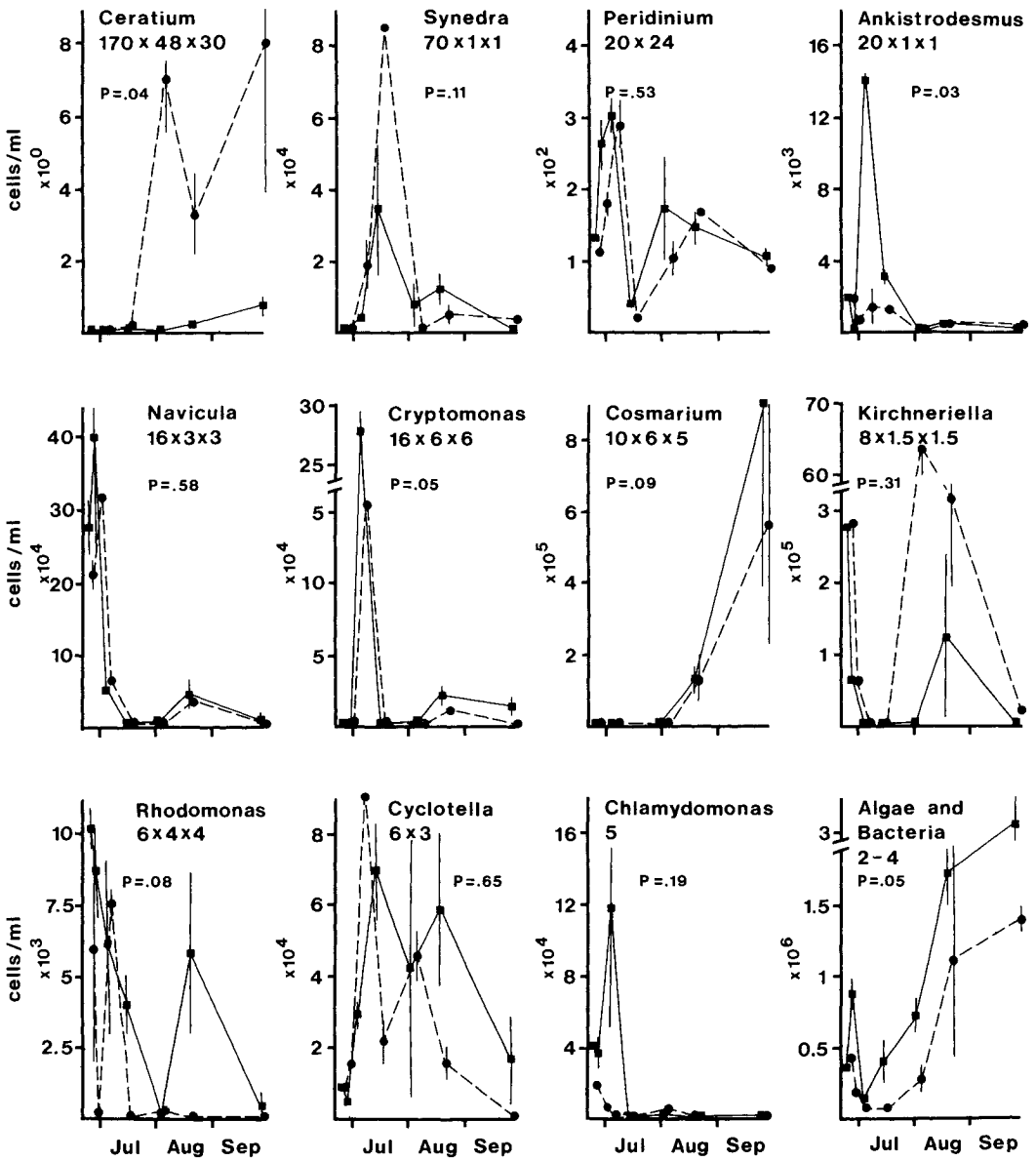
Drenner et al.

Fig. 5. Changes in densities of dominant phytoplankton in ponds containing gizzard shad (solid line) and control ponds without fish (dashed line). Algal length, width, and thickness are shown below the genus. Points—means of replicate ponds; bars—range of observed densities. Probabilities are from the split-plot ANOVA (df = 1,2).

Some limnologists have suggested that more attention should be devoted to the possibility of restructuring biological communities as a direct approach to combating eutrophication (Hurlbert et al. 1972; Sha- piro et al. 1975). One proposal was the reduction of phytoplankton abundance through enhancement of zooplankton grazing brought about by reduction of populations of visual-feeding zooplanktivorous

fish. Although this strategy may suppress nannoplankton, it may not reduce some types of net phytoplankton (Lynch 1980; Lynch and Shapiro 1981) which can be seasonally abundant in eutrophic lakes. Kutkuhn (1957) suggested that gizzard shad may suppress irruptions of objectionable algae, but the potential importance of native filter-feeding fish as determinants of phytoplankton community structure has generally been overlooked. While our study shows that gizzard shad can suppress *Ceratium*, we need more information about their impact on colonial and filamentous blue-green algae to evaluate their potential use for the biomanipulation of phytoplankton populations.

References

ANDERSSON, G., H. BERGGREN, G. CRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia **59:** 9–15.

BAKER, C. D., AND E. H. SCHMITZ. 1971. Food habits of adult gizzard and threadfin shad in two Ozark reservoirs, p. 3–11. *In* Reservoir fisheries and limnology. Am. Fish. Soc. Spec. Publ. 8.

BANSE, K. 1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size—a review. J. Phycol. **12:** 135–140.

BLABER, S. J. M. 1979. The biology of filter feeding teleosts in Lake St. Lucia, Zululand. J. Fish Biol. **15:** 37–59.

BOYD, C. M. 1976. Selection of particle sizes by filter-feeding copepods: A plea for reason. Limnol. Oceanogr. **21:** 175–180.

BRIAND, F., AND E. McCAULEY. 1978. Cybernetic mechanisms in lake plankton systems: How to control undesirable algae. Nature **273:** 228–230.

DeNOYELLES, F., JR., AND W. J. O'BRIEN. 1978. Phytoplankton succession in nutrient enriched experimental ponds as related to changing carbon, nitrogen and phosphorus conditions. Arch. Hydrobiol. **84:** 137–165.

DRENNER, R. W., F. DeNOYELLES, JR., AND D. KETTLE. 1982*a.* Selective impact of filter-feeding gizzard shad on zooplankton community structure. Limnol. Oceanogr. **27:** 965–968.

———, W. J. O'BRIEN, AND J. R. MUMMERT. 1982*b.* Filter-feeding rates of gizzard shad. Trans. Am. Fish. Soc. **111:** 210–215.

———, J. R. STRICKLER, AND W. J. O'BRIEN. 1978. Capture probability: The role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Bd. Can. **35:** 1370–1373.

DURBIN, A. G. 1979. Food selection by plankton feeding fishes, p. 203–218. *In* R. H. Stroud and H. Clepper [eds.], Predator-prey systems in fisheries management. Sport Fish. Inst.

———, AND E. G. DURBIN. 1975. Grazing rates of

the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. **33:** 265–277.

FRYER, G., AND T. D. ILES. 1972. The cichlid fishes of the great lakes of Africa. T.F.H. Publ.

GELLER, W. AND H. MÜLLER. 1981. The filtration apparatus of cladocera: Filter mesh-sizes and their implications on food selectivity. Oecologia **49:** 316–321.

GILL, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. V. 2. Iowa State.

GUNN, J. M., S. U. QADRI, AND D. C. MORTIMER. 1977. Filamentous algae as a food source for the brown bullhead (*Ictalurus nebulosus*). J. Fish. Res. Bd. Can. **34:** 396–401.

HALL, D. S., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. **15:** 839–928.

HURLBERT, S. H., AND M. S. MULLA. 1981. Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. Hydrobiologia **83:** 125–151.

———, J. ZEDLER, AND D. FAIRBANKS. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science **175:** 639–641.

IWATA, K. 1976. Morphological and physiological studies on the phytoplankton feeders in cyprinid fishes. 1. Developmental changes of feeding organs and ingestion rates in kawachibuna (*Carassius auratus cuvieri*), silver carp (*Hypophthalmichthys molitrix*), and nigorobuna (*C. auratus grandoculis*). Jap. J. Limnol. **37:** 135–147.

JENKINS, R. M. 1967. The influence of some environmental factors on standing crop and harvest of fishes in U.S. reservoirs, p. 298–321. *In* Reservoir Fish. Res. Symp. S. Div. Am. Fish. Soc.

KITCHELL, J. F., AND J. T. WINDELL. 1970. Nutritional value of algae to bluegill sunfish, *Lepomis macrochirus*. Copeia 1970, p. 186–190.

KUTKUHN, J. H. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. Trans. Am. Fish. Soc. **87:** 80–103.

LAMARRA, V. A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Int. Ver. Theor. Angew. Limnol. Verh. **19:** 2461–2468.

LYNCH, M. 1980. *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. Am. Soc. Limnol. Oceanogr. Spec. Symp. **3:** 299–304. New England.

———, AND J. SHAPIRO. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. **26:** 86–102.

MURPHY, G. I. 1950. The life history of the greaser blackfish (*Orthodon microlepidotus*) of Clear Lake, Lake County, California. Calif. Fish Game **36:** 119–133.

NAKASHIMA, B. S., AND W. C. LEGGETT. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Can. J. Fish. Aquat. Sci. **37:** 1540–1549.

NIVAL, P., AND S. NIVAL. 1976. Particle retention efficiencies of an herbivorous copepod, *Acartia*

clausi (adult and copepodite stages): Effects on grazing. Limnol. Oceanogr. **21:** 24–38.

O'BRIEN, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. **67:** 572–581.

PORTER, K. G. 1977. The plant-animal interface in freshwater ecosystems. Am. Sci. **65:** 159–170.

ROSEN, R. A., AND D. C. HALES. 1981. Feeding of paddlefish, *Polyodon spathula.* Copeia 1981, p. 441–455.

SCHLESINGER, D. A., L. A. MOLOT, AND B. J. SHUTER. 1981. Specific growth rates of freshwater algae in relation to cell size and light intensity. Can. J. Fish. Aquat. Sci. **38:** 1052–1058.

SHAPIRO, J., V. LAMARRA, AND M. LYNCH. 1975. Biomanipulation: An ecosystem approach to lake restoration, p. 85–96. *In* Water quality management and biological control. Proc. Symp. Univ. Fla.

SMITH, R. E., AND J. KALFF. 1982. Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton. J. Phycol. **18:** 275–284.

SMITH, W. L. 1963. Viable algal cells from the gut of the gizzard shad *Dorosoma cepedianum* (Le-Sueur). Proc. Okla. Acad. Sci. **43:** 148–149.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman.

SOMMER, U. 1981. The role of *r*- and *K*-selection in the succession of phytoplankton in Lake Constance. Acta Oecol./Oecol. Gen. **2:** 327–342.

STAROSTKA, V. J., AND R. L. APPLEGATE. 1970. Food selectivity of bigmouth buffalo, *Ictiobus cyprinellus,* in Lake Poinsett, South Dakota. Trans. Am. Fish. Soc. **99:** 571–576.

VELASQUEZ, G. T. 1939. On the viability of algae obtained from the digestive tract of the gizzard shad, *Dorosoma cepedianum* (Le Sueur). Am. Midl. Nat. **22:** 376–412.

WINER, B. J. 1971. Statistical principles in experimental design. McGraw-Hill.